First bipolar benthic brooder

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ABSTRACT: A bipolar distribution is one in which a taxon occurs at high northern and southern latitudes but is absent in the latitudes between. In spite of the large distance between the Arctic and Antarctic, there are records of biota with bipolar distributions, both currently and in the geological past. To date, combined morphological and genetic studies of organisms such as bacteria and foraminifera have confirmed the occurrence of some species in both polar regions. Bipolar genera and families are also known in larger invertebrates, e.g. in crustaceans and molluscs, and a recent Census of Marine Life report suggested that more than 200 metazoan species may have bipolar distributions. Here we investigated specimens of the the cheilostome bryozoan *Callopora weslawski* from both Arctic and Antarctic localities. To our knowledge this is the first benthic brooder to be found in both polar regions and is the first record of a species of *Callopora* in Antarctic waters. We used scanning electron microscopy and statistical analyses to confirm the morphological identity of individuals. The encrusting nature of the species, its distribution in the deep Weddell Sea and its rarity mean that genetic confirmation of bipolarity may take years or decades. Possible paths of distribution are discussed, including the Pangea break-up, Plio-Pleistocene glaciations, isothermal submergence via off-shelf or abyssal currents and anthropogenic transport.

KEY WORDS: Bipolar · Arctic · Antarctic · Bryozoa · Biodiversity

INTRODUCTION

The bipolar distribution of biota is defined as the spread over a region in the high Northern and Southern Hemispheres, with a gap between the two (Ekman 1953, Stepanjants et al. 2006). Here we consider extreme bipolarity between the 2 polar regions. The Arctic and Antarctic regions share many similar environmental characteristics, including extreme seasonal light fluctuation supply, low water temperature, strong mixing and cold dense water production at the surface, seasonal sea-ice, benthic scour by icebergs, ice shelves and cyclical expansion and retreat of ice sheets during glaciations. However, the 2 polar regions also differ in many ways, such as in their structure (Antarctica is a continent surrounded by ocean, compared with ocean surrounded by continents in the Arctic), level of isolation, bathymetry and especially their geological histories. Following near-complete eradication of polar shelf faunas during the last glaciation, the Arctic has been reinvaded since the ice sheet retreat (about 14 000 yr ago), mostly by biota of Atlantic and Pacific origin (and thus is geologically young, see Dunton 1992). In contrast, most Antarctic shelf fauna are endemic (Arntz et al. 1997) and have had little recent exchange with taxa in Atlantic, Indian and Pacific Oceans (e.g. see Hunter & Halanych 2008) and so are likely to have recolonised from a combination of refugia, continental slopes or outlying archipelagos. A number of vertebrates (such as whales, seals and birds) migrate between the poles, but otherwise the distance between polar regions is considerable for most mega-, macro- and smaller fauna, even during glacial maxima (ice ages).

In spite of the 12 000 km minimum distance (from the Polar Front north of South Georgia to the Labrador Sea) and major temperature or bathymetric extremes between the 2 polar regions, there are a number of

records indicating potential bipolar biota distributions and/or exchanges both in the geological past and in recent times (Lindberg 1991, Crame 1993, Stepanjants et al. 2006, Pawlowski et al. 2007). This was first observed more than 150 yr ago (e.g. Ross 1847). Recent molecular studies have indicated strong genetic similarity of some widely distributed foraminifera, such as those which occur from the Arctic to Antarctic, from pelagic to deep bottom sea realms (Darling et al. 2000, Pawlowski et al. 2007). However in larger invertebrates, bipolar records are mainly at the genus or family level (see Crame 1993, Jazdzewski et al. 1995). Recently, the Census of Marine Life and Census of Antarctic Marine Life highlighted at least 235 species (including worms, crustaceans, pteropods, birds and whales) that have been reported from both polar regions. In the present study we present the first record of the occurrence of a cheilostomous bryozoan (*Callopora weslawski* Kuklinski and Taylor, 2006) in both the Arctic and Antarctic. This is also the first record of *Callopora* species within the Polar Front (Antarctic waters) (see Hayward 1995). As with other phyla (e.g. molluscs), there are, however, many bipolar bryozoan genera already known from the Arctic and Antarctic (e.g. *Escharella*, *Microporella*, *Amphiblestrum*) (see Kluge 1975, Hayward 1995). Previous putative records of bryozoan species (e.g. *Idmidronea atlantica*, *Microporella ciliata*) reported in both polar regions have been found, on closer morphological examination, to be previously undescribed species restricted in distribution to either the Arctic or Antarctic, or misidentifications (Moyano 1982, Hayward & Ryland 1990, Ostrovsky & Taylor 1996, Kuklinski & Taylor 2008a).

In contrast to previously confirmed bipolar species, all of which are migratory or mobile to some degree, the bryozoan *Callopora weslawski* is a sessile animal with low dispersal potential. Its reproductive strategy involves the production of lecithotrophic larvae typically able to stay in the water column from a few minutes to hours, rarely up to 5 d prior to settlement and metamorphosis (Ryland 1974, Cook & Chimonides 1985). The exact larval duration of *C. weslawski* is unknown, and Antarctic cheilostomes may have longer larval development and durations than those elsewhere (Barnes & Clarke 1998), but even days or weeks would not enable dispersal of thousands of kilometres, especially from north to south (as the strongest Antarctic current is circumpolar). This suggests that the potential for colonization of new areas is very limited. Here we compare morphological characters of individuals of *C. weslawski* from Arctic and Antarctic samples and we discuss possible mechanisms of species transfer between 2 such extremely distant localities.

MATERIALS AND METHODS

Callopora weslawski appeared in the literature for the first time in 1916 under the name *Membranipora whiteavesi*, recorded in northeast Greenland (Levinsen 1916). The species was also misidentified later as *C. whiteavesi* by several other authors including Kluge (1975) and Gostilovskaya (1978). Recent scanning electron microscopy (SEM) revealed this species to be undescribed (Kuklinski & Taylor 2006). According to the literature, this is a circumarctic species (Kluge, 1975) and confirmed records to date (with SEM analysis) include East Greenland, Spitsbergen, Franz Joseph Land and the Kara Sea (Kuklinski & Taylor 2006, Kuklinski & Bader 2007). In the Arctic, the species has been recorded as deep as 500 m, but seems to be most common and abundant between 100 and 300 m (Kluge 1975, Kuklinski & Taylor 2006). This species has been confirmed on rocks, shells and other hard objects, but the scarcity of reports suggests that it has not been recorded as common anywhere to date (Kluge 1975). For more details of Arctic material examination and taxonomic description, see Kuklinski & Taylor (2006).

Antarctic material was collected during the R/V 'Polarstern' expeditions to the Weddell Sea between 2005 (ANDEEP III: Antarctic DEEP sea) and 2007 (ANDEEP SYSTCO: Antarctic DEEP sea, SYSTem Coupling). Two colonies were found, one at 2190 m on a rock (70° 04.58′ S, 03° 19.66′ W) and the other at 1030 m on a sabellariid polychaete tube (71° 18.35′ S, 13° 57.71′ W). SEM of all the material was undertaken with a low-vacuum instrument (LEO 1455-VP) capable of imaging large, uncoated specimens using back-scattered electrons. Zooecial measurements were made on SEM images using the software ImageJ.

The study material is lodged in the Natural History Museum, London and the Zoological Institute of the Russian Academy of Sciences, St. Petersburg.

Similarities in zooid and ovicell length to width ratios of individuals from the Arctic and Antarctic were analysed using 1-way ANOVA. Data were log-transformed prior to analysis to improve normality and homogeneity.

RESULTS AND DISCUSSION

The present study represents the first record of a benthic brooding organism, the bryozoan *Callopora weslawski*, occurring in both the Arctic and Antarctic. Although bipolarity among marine bryozoans was discussed as early as 1904, no species in particular were mentioned (Calvet 1904). Recent species of Calloporidae are distributed worldwide across all climatic zones, from the poles to the tropics. However, species

of the genus *Callopora* seem to be limited in their distribution to Northern Hemisphere with no records from the tropical zone (Bock 2009). Our morphological analysis, using SEM, shows that both Arctic and Antarctic individuals are similar (Fig. 1). Zooid size of specimens did differ between individuals from the Arctic and Antarctic, but their general morphological appearence was similar (Table 1, Fig. 1). Zooid length to width ratio and ovicell length to width ratio were not significantly different between individuals from both polar seas (ANOVA, $F_{1, 24} = 1.001$, p = 0.327, and $F_{1, 6} = 0.005$, p = 0.944, respectively) (Table 1). Additionally, individuals of *C. weslawski* from the Arctic and Antarctic share the following similarities: small, transversely elliptical pore chambers facing frontally, laterally and distolaterally; finely pustulose narrow cryptocysts, sloping downward; elliptical or oval opesia; circumopesial mural spines, as well as spines arising outside the mural rim on lateral gymnocysts; uncalcified ovicell ectoocium, apart from a narrow crescent around lateral and distal perimetry; and finely pustulose entoocium. Some Antarctic individuals seem to have a broader cryptocyst than Arctic specimens. Also, opesia are often pear-shaped in Antarctic individuals. Although these characters seem to be more frequent in Antarctic individuals, they have also been recorded in specimens from the Arctic.

Differences in zooid size and opesia shape and, generally, phenotypic variation in colonial animals can often be ascribed to factors such as microenvironment, ontogeny and astogeny (Boardman & Cheetham 1973, Schopf 1976, Hageman et al. 1999). The Antarctic specimens are one-third smaller than those in the Arctic, but this could be due to these (small) colonies still being at the stage of astogenetic change. Zooid size may still increase through early colony development and then level off (zone of astogenetic repetition); however, since there were already some zooids with ovicells (structures in which embryos develop), at least one colony appears to have been reproductively mature. Thus differences related to ontogeny or astogeny
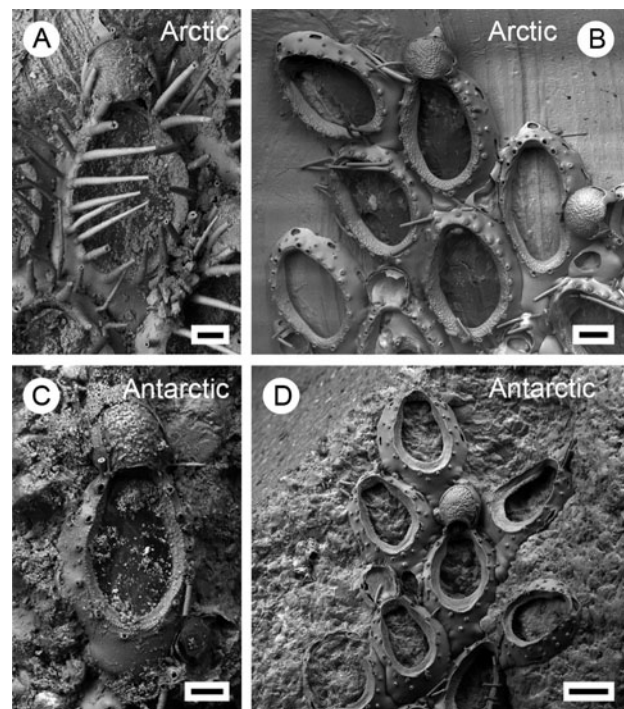

Fig. 1. *Callopora weslawski* Kuklinski and Taylor, 2006. (A) Arctic (Kara Sea, Holotype: Zoological Institute, ZN 20/3101), ovicellate zooid, unbleached. (B) Arctic (Holotype: ZN 20/3101) autozooids and ovicellate zooid at the the growing edge, bleached. (C) Antarctic (71° 18.35′ S, 13° 57.71′ W; 1030 m depth; unfortunately this specimen was damaged during bleaching and only SEM images of unbleached material exist for this individual) ovicellate zooid on a sabellariid tube, unbleached. (D) Antarctic (70° 04.58′ S, 03° 19.66′ W; 2190 m depth; Natural History Museum 2009.6.12.1) autozooids and ovicellate zooid at the the growing edge, bleached. Scale bars: (A,C) 100 µm; (B,D) 200 µm

(colony development) can be ruled out. Several studies have shown that, even within species, zooid size can be influenced by seawater temperature, both in natural habitats and under laboratory conditions. There are also indications that zooid size varies with latitude (between colonies of the same species), which is probably driven by water temperature (Silén & Harmelin 1976, Kuklinski & Taylor 2008b) or possibly oxygen levels as a consequence of temperature (Hunter & Hughes 1994, O'Dea & Okamura 1999). The numbers of circumopesial mural spines and spines arising outside the mural rim seem to vary both within and between colonies of *Callopora weslawski*. These, therefore, are not stable taxonomical characters that could separate individuals from the Arctic and Antarctic into separate species. However, on average, a similar number of

Table 1. *Callopora weslawski*. Measurements of zooidal characteristics of Arctic and Antarctic bryozoan specimens (mean ± SD, number of measurements in parentheses)

Zooidal characteristic	Arctic	Antarctic
Zooid length (mm)	0.92 ± 0.08 (15)	0.54 ± 0.04 (11)
Zooid width (mm)	0.56 ± 0.03 (15)	0.34 ± 0.03 (11)
Zooid length:width ratio	1.65 ± 0.17 (15)	1.56 ± 0.21 (11)
Ovicell length (mm)	0.25 ± 0.01 (4)	0.17 ± 0.02 (4)
Ovicell width (mm)	0.29 ± 0.02 (4)	0.20 ± 0.01 (4)
Ovicell length:width ratio	0.86 ± 0.13 (4)	0.86 ± 0.12 (4)
No. circumopesial mural spines	13–18 (9)	12–16 (10)
No. spines located outside mural rim	5–10 (7)	4–12 (7)

spines were found in individuals both from the Arctic (7) and Antarctic (8). The species occurs in both polar regions on similar firm substrates, typically rocks.

Ideally, morphological evidence of specimens comprising the same species would be supported by genetic investigation (at nuclear and mitochondrial loci). This requires immediate preservation in an appropriate solution, e.g. ethanol. However, this is problematic for cryptic lithophyllic taxa such as encrusting cheilostomes. They often occur on boulders too large for immersion in solution and their occurrence is not obvious without close inspection of the entire boulder surface. Additonally, they are not identifiable even to family or genus without stereomicroscopic examination. Thus most encrusting species collected using trawled apparatus are often only discovered after they are no longer viable for genetic analyses. Nevertheless, trawled bryozoan species may be preserved appropriately for genetics when they occur on smaller rocks and treatments are applied immediately to whole catches, such as when using EpiBenthic Sledges (see Kaiser et al. 2008). None of the *Callopora weslawski* specimens from deep Weddell Sea samples are viable for genetic testing, nor are any other deep Southern Ocean bryozoan species reported to date (e.g. see Gontar & Zabala 2000).

Possible mechanisms of bipolar occurrence

Discontinuities in the distribution of marine taxa were recognized in the modern ocean at least 150 yr ago (e.g. Darwin 1859). Fossil assemblage analyses suggest that bipolarity cannot be linked to just one major event in geological history, e.g. the Pangea break-up or Plio-Pleistocene glaciations (Crame 1993). There are suggestions that organisms from both hemispheres may have been able to breach the tropics repeatedly during the last 200 million yr (Lindberg 1991, Crame 1993, Stepanjants et al. 2006). Since the earliest fossil record of a member of Calloporidae, to which *Callopora weslawski* belongs, is from the Late Albian (ca. 100 million yr ago [mya]) (Taylor 1993, Ostrovsky et al. 2008), some geological events are unlikely as causal mechanisms underlying a bipolar distribution in this case. Establishment of a bipolar distribution of *C. weslawski* due to the Mesozoic fragmentation of Pangea (200 mya) is highly unlikely, not least because species rarely survive more than 10 million yr (Stanley 1975) and disjunct populations are unlikely to remain as one species without connectivity for such a considerable period. There were a number of more recent global cool phases in the geological past: e.g. Tithonian–Berriasian (ca. 145 mya) and Late Albian (ca. 100 mya). Crame (1993) suggested that cool phases may have led to the widespread distri-

butions of certain ancestral taxa. Increased Southern Hemisphere sea surface temperatures through the Miocene from 6 to 12°C (see Zachos et al. 2001) increased latitudinal provinciality for a variety of planktonic taxa in both the Atlantic and Pacific Ocean basins (Lindberg 1991, Darling et al. 2000). These climatic and oceanographic changes may well have led to the establishment of a bipolar pattern of distribution of families and genera. Transequatorial transit and subsequent genetic exchange is likely to have increased during cooling periods associated with glacial cycling in the Quaternary period (the past 1.8 million yr). Low-latitude sedimentary records indicate the presence of subpolar planktonic foraminifera within the equatorial zone during these cooling cycles (McIntyre et al. 1989). Another possibility driving bipolar distributions is isothermal submergence, that is, passage through the tropics via off-shelf or abyssal currents (Stepanjants et al. 2006). The Weddell Sea (where *C. weslawski* specimens were sampled in the Antarctic) is a key source of Antarctic Bottom Water, which provides much of the deep water of the World Ocean. This water mass has been traced as far north as 56°N in the Atlantic Ocean (New & Smythe-Wright 2001). Individuals of *C. weslawski* have been found in deep samples from both polar regions, which suggests that a deep transit might be a physiological and ecological possibility. The brief larval duration of species like *C. weslawski* would require many generations to travel so far. Although adults are sessile and larvae have a very short planktonic phase, their potential for travel may still be considerable because they encrust objects that may be carried in currents (such as polychaete worm tubes, which can break from attachment points). Futhermore, the life span of colonies may be considerable, allowing a single genetic individual to travel long distances.

Anthropogenic transport (e.g. widespread transport of fouling organisms in ship ballast waters) seems unlikely. In both areas, the species occur only in deep water (Arctic, down to 500 m; Antarctic, 1000 to 2000 m), thus recruitment onto ship hulls or occurrence in ballast water seems highly improbable.

Molecular techniques may prove the species from the Antarctic to be an undescribed cryptic species. However, there are now many examples in which disjunct morphospecies were found to be identical on a genetic level. For example, Darling et al. (2000) and Pawlowski et al. (2007) have found complete sequence identity between Arctic and Antarctic morphospecies of pelagic and benthic foraminifera, respectively. On the other hand, Pawlowski et al. (2008) were able to show genetic differentiation between morphologically identical Arctic and Antarctic monothalamous foraminifera. The widely distributed (but not bipolar) *Celleporella hyalina* complex is an example of a cheilostome

bryozoan where morphologically similar species were separated into sibling species both using molecular and mating experiments (Gomez et al. 2007a,b). Morphological identity can be due to convergent or parallel evolution in similar environments, yet Briggs (1987) suggests that many species which currently persist with a discontinuous distribution and show little morphological divergence are likely to have had relatively recent interchange. In the case of *Callopora weslawski*, the level of morphological identity between individuals from the Arctic and Antarctic suggests that individuals are either of the same species or are at least sister species derived from a closely related ancestor. *C. weslawski* seems to be the strongest candidate to date of a bipolar benthic brooder.

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